

# Sag-Mediated Modulated Tension in Terebellid Tentacles Exposed to Flow

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**Abstract.** The long, compliant feeding tentacles of the terebellid polychaete *Eupolyornia heterobranchia* not only stretch out over a sandflat substratum but also extend into flow. Tentacles suspended perpendicular to flow responded to increasing velocity by increasing their sag. An analysis of tension in these tentacles, mathematically analogous to that applicable to suspension bridges, shows that sagging permits the tentacles to avoid increases in tension that would otherwise occur as flow increases. Force modulation was achieved by active muscular control rather than by passive material properties. Although these tentacles would certainly break in the experimental flows if they did not sag, the low tension achieved suggests that some other reason, such as limitations on the adherence of cilia and mucus, accounts for the level of tension observed. Because drag is maximum on tentacles oriented perpendicular to flow, reorientation of tentacles, either by sagging or by dangling parallel to flow, additionally reduces tension by reducing drag. Theoretical estimates of drag on tentacles oriented parallel to flow show that they are never in danger of being broken. Drag is sufficient, however, to assist in passive extension of tentacles. While reorientation is a common mode of drag reduction among marine organisms, sagging represents a novel mechanism of mediating structural forces resulting from flow.

## Introduction

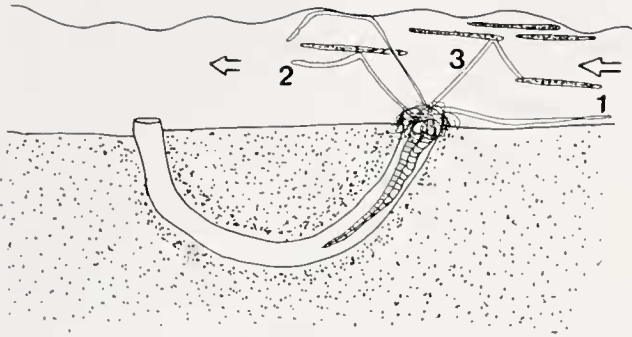
Reliance upon a particulate food resource is common among marine invertebrates, and tentacles are among the most versatile of structures used to capture such food. The mechanical demands on tentacles during feeding vary widely depending on the way that tentacles are used, and the mechanical characteristics of the tentacles constrain

the ways that tentacles can be used by animals during feeding.

The mechanical demands on the tentacles used to capture suspended food consist largely of resisting the drag forces exerted upon them by flow. Although there is a range in mechanical characteristics of tentacles specialized for capturing suspended food, typically the tentacles that are used exclusively for suspension feeding are relatively inextensible. Bryozoans, for example, extend a short, stiff crown of tentacles into flow to capture suspended particles.

In contrast, the deposit feeding terebellid polychaetes feed off the surface of the substratum surrounding their tubes by means of numerous, long compliant tentacles. Most terebellids remain within their tubes, so that the area of substratum over which they can feed is limited by the length of their tentacles. During the process of feeding, force is required to pull the tentacles out, to keep them out, and to pull the tentacles back in. Terebellids exert the force to extend their tentacles, at least partially, by means of cilia located in a ventral ciliated food groove. To do this, they flatten the food groove against the substratum and use the cilia to crawl. Mucus in the food groove, in addition to its role in particle adhesion and transport, helps the tentacles to adhere to surfaces. The existence of circular muscles surrounding a fluid-filled tentacular coelom indicates that terebellids may also use internal hydrostatic pressures to help generate the forces required to extend their tentacles.

The present study examines a terebellid polychaete, *Eupolyornia heterobranchia*, that extends tentacles not only over the substratum, but also into flow. *E. heterobranchia* individuals found on False Bay, San Juan Island, Washington suspend their tentacles between layers in dense mats of the sheet-like green alga *Ulva fenestrata* (Fig. 1). The forces exerted on these tentacles include those required to extend the tentacles over the surface of the substratum and flow-induced drag on suspended tentacles.



**Figure 1.** Schematic drawing (not to scale) of the terebellid *Eupolymnia heterobranchia* in its natural habitat. Arrow indicates direction of flow. *E. heterobranchia* (1) extends tentacles out over substrata, (2) dangles the ends of tentacles parallel to flow, and (3) suspends tentacles at an angle to flow by attachment either to sheet-like fronds of *Uva fenestrata* or to the water surface.

Tentacles exposed to flow between two points of attachment sag in the direction of flow (Fig. 2), much as the cables of suspension bridges sag in the direction of gravitational forces. The similarity is such that the equations used to analyze tension in the cables of suspension bridges are appropriate for analyzing tension in the tentacles of *E. heterobranchia* oriented perpendicular to flow. Such an analysis is used to address the specific question: how do the behavior and mechanical characteristics of the tentacles of the terebellid polychaete *Eupolymnia heterobranchia* allow them to remain suspended in flow? The results of these experiments represent one step in understanding the association between the mechanical characteristics of feeding tentacles and the way that they are used for feeding.

### Materials and Methods

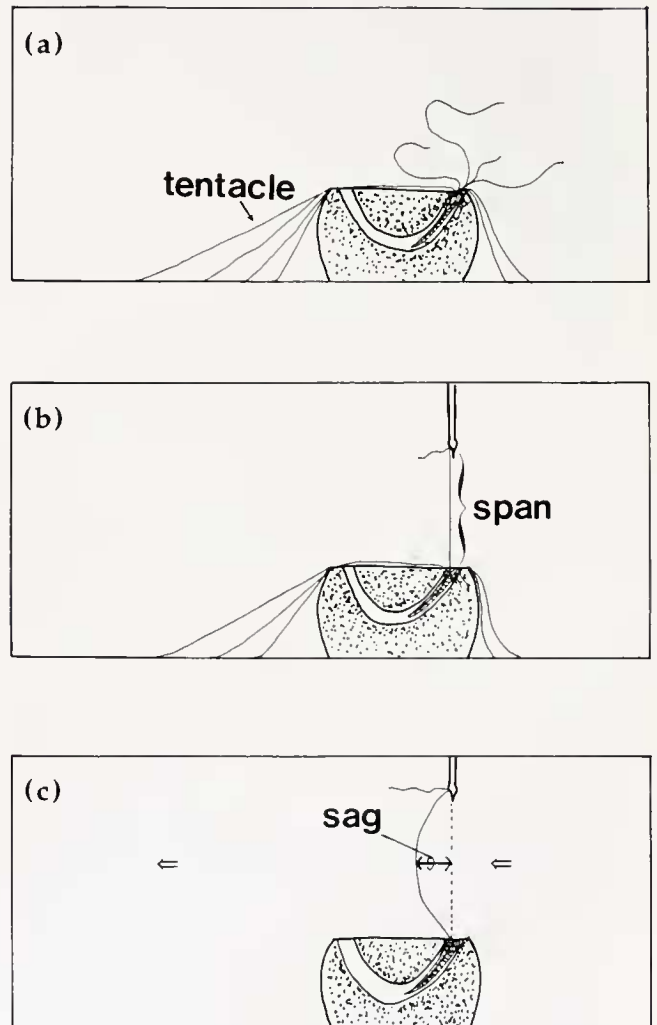
#### Field site and collection of terebellids

*Eupolymnia heterobranchia* specimens were collected from the False Bay tidal flat on San Juan Island, Washington (48° 29' N; 123° 04' W) at about 0.0 m mean lower low water within areas covered by extensive mats of *Uva fenestrata*. These layered mats occur annually and persist from May through October (Price and Hylleberg, 1982). The unattached thalli of *U. fenestrata* float above the substratum when the flat is submerged. *E. heterobranchia* commonly construct tubes within folds in these floating algal sheets rather than within the mud of the flat. Whether they construct their tubes within the mud or the algal mats, these terebellids suspend their tentacles between the layers of algal thalli and into flow (Fig. 1).

False Bay is characterized by tidally dominated, unidirectional flow. Flow averaged over five days in a slightly more exposed area of False Bay (east side, near site C in

Price and Hylleberg, 1982) was  $0.043 \text{ m s}^{-1}$ ; daily peak velocities ranged between  $0.10$  and  $0.20 \text{ m s}^{-1}$  (Pentcheff, unpubl. data; measured in the field by a Marsh-McBirney electromagnetic flow probe at 6 cm above a rock substratum). Flow over the relatively protected area where *E. heterobranchia* was collected (west side, site D in Price and Hylleberg, 1982) and particularly between the layers of *U. fenestrata*, should be comparable, although somewhat slower.

Once collected, *E. heterobranchia* individuals were maintained at the University of Washington's Friday



**Figure 2.** Schematic drawing (not to scale) of *Eupolymnia heterobranchia* in a flow tank. (a) Animals were allowed to self-attach a tentacle to the probe (using cilia and mucus). (b) Raising the probe oriented the tentacles perpendicular to flow. Span was the distance between points of attachment. (c) Arrow indicates direction of flow. Sag was the distance between the vertical line drawn between points of attachment and the point of maximum sag.

Harbor Laboratory in circulating seawater tables at around 15°C. When possible, worms were kept in their original tubes. Those specimens of *E. heterobranchia* that lost their original tubes were placed on muddy sediment where they constructed new (flimsier) tubes.

### The parabolic cable equation

The tension (force) in suspended tentacles that results from drag can be estimated with engineering formulas used to calculate tension in the cables of suspension bridges. Tension in the cables of suspension bridges is calculated using the force acting on the cables, the distance (or span) between points of attachment of the cable, and the amount of sag in the cable. Below, I review briefly the standard engineering equations for tension in parabolic cables (those that carry a uniform distributed load; see Steinman, 1942).

The horizontal tension at the points of attachment of a cable is exactly the tension in the cable at the point of maximum sag. At this point, there is only a horizontal component to the tension, and no vertical component. The horizontal tension,  $H$ , is:

$$H = \frac{\omega L^2}{8f} \quad (1)$$

where  $\omega$  for a parabolic cable is the uniform distributed load (a force) per horizontal linear unit,  $L$  is the span distance between points of attachment of the cable, and  $f$  is the sag of the cable. Sag of a cable is defined as the distance between the lowest point and a horizontal line drawn between the points of attachment of the cable.

The maximum tension,  $T$ , in the cable occurs at the points of attachment, where there is the greatest summed contribution from the vertical component of tension. The maximum tension,  $T$ , can be calculated from the horizontal tension,  $H$ , as follows (Steinman, 1942):

$$T = \sqrt{\left(\frac{\omega L}{2}\right)^2 + H^2} \quad (2)$$

Maximum tension can also be expressed as a function of the ratio of span to sag, ( $L/f$ ), by substituting Eqn (1) into Eqn (2) for  $H$ :

$$T = \sqrt{\left(\frac{\omega L}{2}\right)^2 + \left(\left(\frac{\omega L}{8}\right)\left(\frac{L}{f}\right)\right)^2} \quad (3)$$

Similar to the parabolic cable of suspension bridges, where the cable carries a uniformly distributed gravitational load, drag exerts a force that acts along the horizontal distance (projected area) of a tentacle oriented perpendicular to flow and suspended between two points of attachment. Therefore, force, which is  $\omega L$  for the parabolic cable, is drag,  $D$ , in the tentacle-cable equation. The de-

termination of drag on the tentacles of *E. heterobranchia* and its use in the cable equation are described below.

### Drag calculations

Drag is greatest on a tentacle oriented perpendicular to flow (Vogel, 1981). To orient tentacles perpendicular to flow, specimens of *E. heterobranchia*, intact within their tubes, were buried in mud in glass dishes that were placed in the bottom of a recirculating seawater flow tank (similar in design to that of Vogel and LaBarbera, 1978) (Fig. 2a). A micromanipulator was used to lower a probe to the mouth of the worm's tube and, subsequently, to raise the probe after the worm had attached a tentacle using cilia and mucus. In this way, tentacles were oriented perpendicular to the direction of flow, with two points of attachment: one on the probe, the other on the body of the worm (Fig. 2b). The tip ends of these suspended tentacles usually dangled downstream from the point of attachment to the probe (Fig. 2c).

Behavior of the tentacles in response to flow was quantified by photographing each tentacle several times at each velocity with a camera oriented perpendicular to the sag. A known distance on the probe was used to determine scale in all photographs. Span ( $L$ ), sag ( $f$ ), and tentacle length ( $l$ ) were measured off photographs; where span was the distance between points of attachment of a tentacle (Fig. 2b), sag was the distance between the maximum sag (parallel to flow) in that tentacle and a line defined by the two points of attachment (Fig. 2c) and tentacle length was the real length of the tentacle between the points of attachment. The span was set at a minimum by this method (no lower than the tip of the probe), but a tentacle could increase or decrease its span by changing attachment points along the length of the probe.

Drag on tentacles was determined using the standard equation for the drag on a cylinder perpendicular to flow (Vogel, 1981):

$$D = \frac{1}{2} C_D \rho S U^2 \quad (4)$$

where  $D$  is drag,  $C_D$  is the drag coefficient,  $\rho$  is the density of seawater,  $S$  is the projected area of each tentacle perpendicular to flow and  $U$  is the velocity. The projected area,  $S$ , of each tentacle was calculated as  $L \times d$ ; where  $d$  was the tentacle diameter. Tentacle diameter,  $d$ , was measured on 31 living, unstretched tentacles under a compound microscope (mean = 0.10; minimum = 0.05 mm; maximum = 0.13 mm; SE = 0.003 mm). Because diameter could not be measured during experiments in the flow tank, this mean tentacle diameter was used in all calculations of tension, except as described below. A propagation of error analysis using the minimum and maximum diameters measured indicated that this resulted in a maximum error of  $\pm 15\%$  in the tension estimated



for any particular tentacle. The average error from this source was unbiased.

The conventional drag coefficient,  $C_D$ , was estimated from an empirical formula (for Reynolds numbers from unity to  $10^5$ ) for a cylinder oriented perpendicular to flow (White, 1974 cited in Vogel, 1981):

$$C_D = 1 + 10 \text{Re}^{-2/3} \quad (5)$$

where Re is the Reynolds number:

$$\text{Re} = \rho dU/\mu \quad (6)$$

where  $d$  is the diameter of the tentacle and  $\mu$  is the dynamic viscosity of seawater. Unless otherwise specified, all references to drag in this paper refer to the calculation of drag using the variables as described above.

All experimental velocities in the flow tank were determined by timing neutrally buoyant particles. Experiments were conducted at velocities ranging between 0.5 and 7.0  $\text{cm s}^{-1}$ ; these velocities corresponded to Reynolds numbers for the tentacles between 1 and 7. Tentacles did not remain attached to the probe at velocities greater than 7.0  $\text{cm s}^{-1}$ . These velocities fell within the range measured in the field.

#### Use of the cable equation for the tentacles

Drag was used to calculate the maximum tension in the tentacle by substituting  $D$  for  $\omega L$  in Eqn (3):

$$T = \sqrt{\left(\frac{D}{2}\right)^2 + \left(\left(\frac{D}{8}\right)\left(\frac{L}{f}\right)\right)^2} \quad (7)$$

From Eqn 7 it can be seen that tension is a function of drag as well as of the ratio between span and sag ( $L/f$ ).

#### Material tests

The material properties of the tentacles of *E. heterobranchia* were determined by performing force-extension tests on an Instron tensometer (University of British Columbia, Vancouver). Lengths of tentacles, freshly cut off live animals, were fastened to grips, and relaxed by immersion in a solution of 7.5%  $\text{MgCl}_2$ . After relaxation, grips were moved slowly apart until the tentacle was put nearly into tension. The original length of the tentacles between the grips ( $l_0$ ) was determined by reading the value off the Instron to the nearest 0.1 mm. Tentacles were pulled at constant speed of 50  $\text{mm min}^{-1}$  (= a strain rate of between 0.04 and 0.15  $\text{s}^{-1}$ ; mean = 0.09, SE = 0.006) until they broke. Breaking force was measured off the chart paper to the nearest  $\mu\text{N}$ ; breaking length ( $l$ ) was measured off the chart paper to the nearest 0.1 mm. Extension ratio ( $\lambda$ ) was calculated as  $(l/l_0)$ . Extension ratio is useful as an intuitive description of length changes be-

cause  $\lambda = 2$  corresponds to a doubling of length,  $\lambda = 3$  corresponds to a tripling of length, etc. True strain can be determined from the extension ratio as  $\ln \lambda$  (Vincent, 1990). Linear regression analysis revealed that, within the range of strain rates used in these experiments, both breaking force and breaking  $\lambda$  were independent of strain rate [breaking  $\lambda$ :  $f_{(1,24)} = 2.39$ ,  $P$  (that the slope is zero) = 0.14; breaking force:  $f_{(1,24)} = 0.22$ ,  $P = 0.64$ ].

#### Sag-related drag reduction

It is assumed above that the drag of a sagging tentacle is equal to that of a non-sagging tentacle of equal span oriented perpendicular to flow. I used drag on a tentacle perpendicular to flow to isolate the effects of tension-reduction due to the geometry of sagging (the cable equation) from the drag reducing effects of sagging described below. In fact,  $C_D$  (Eqn 5) will be an overestimate of the coefficient of drag for a sagging tentacle because portions of the tentacle are oriented at some smaller (lower drag) angle to flow. The greater the sag of the tentacles, the greater the degree to which the coefficient of drag is overestimated by  $C_D$ . Furthermore, in a constant volume tentacle, diameter will decrease with increasing sag (increasing stretch). The magnitude of these two sag-related mechanisms of drag reduction can be calculated as follows.

The coefficient of drag for a cylinder at some angle to flow,  $C_{D\theta}$ , can be determined from  $C_D$  (for Reynolds numbers to  $10^5$ ; Hoerner, 1965) by:

$$C_{D\theta} = C_D \cos^3 \theta \quad (8)$$

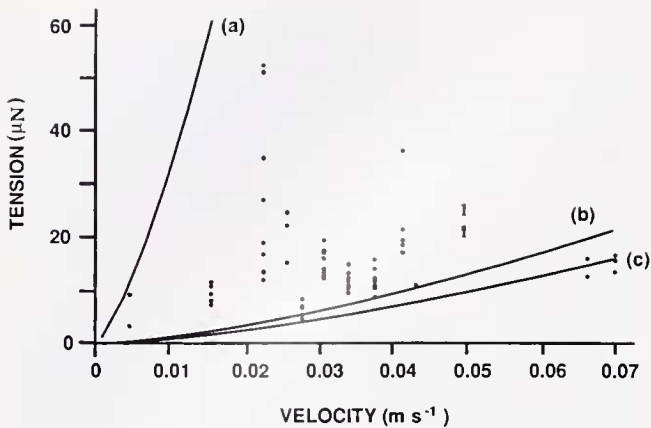
where  $\theta$  is the smallest angle between a line perpendicular to flow and the surface of the tentacle. The angle  $\theta$  was obtained at each point on the tentacle by:

$$\theta = \arctangent \frac{d}{dx} \left( \frac{4fx^2}{L^2} \right) \quad (9)$$

where  $x$  is the distance along the span from the origin (at the point of maximum sag) and  $(4fx^2/L^2)$  is the parabolic equation describing the sagging tentacles (Steinman, 1942). An estimate of the corrected coefficient of drag for the entire tentacle,  $C_{De}$ , was obtained by substituting Eqn 9 into Eqn 8 for  $\theta$ , integrating Eqn 8 over the span of the tentacle (*i.e.*, adding up the coefficient of drag for each infinitesimal piece of tentacle) and dividing by the span of the tentacle:

$$\frac{2C_D \int_0^{L/2} \cos^3 \theta dx}{L} \quad (10)$$

This is similar to the method used to determine the drag coefficient of a wing from the sum of the local drag coefficients of infinitesimal sections of the wing (Abbott and Von Doenhoff, 1959).



**Figure 3.** Tension ( $\mu\text{N}$ ) of suspended tentacles of *Eupolyornia heterobranchia* as a function of velocity ( $\text{m s}^{-1}$ ). Points indicate data. Tension in these tentacles was independent of velocity. Lines indicate tension calculated from Eqn 7 using the mean span and (a) the highest value for  $L/f$ , (b) the lowest value for  $L/f$ , and (c) the lowest value of  $L/f$  and the drag corrected for either the coefficient of drag or both the coefficient of drag and the tentacle diameter. These lines indicate that tension in the tentacles is reduced by sagging, mostly due to geometry (compare b to a) but also partly due to drag reduction (compare b to c).

A corrected diameter,  $d_c$ , was estimated by assuming that the tentacles maintain a constant volume as they stretch:

$$d_c = d(\lambda)^{-0.5} \quad (11)$$

where  $\lambda$  was determined from the ratio of the total length of the tentacle,  $l$  (measured from the photographs), and the span of the tentacle ( $L = l_0$ ).

## Results

### Tentacles as cables

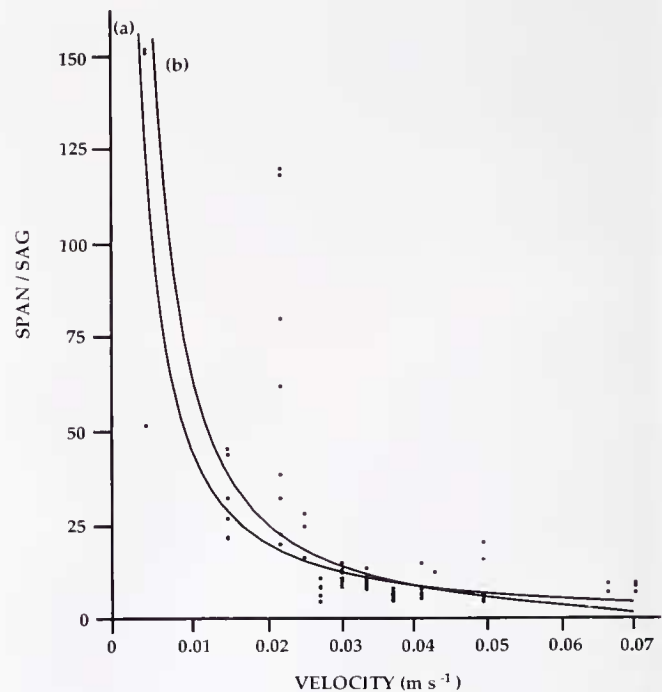
Calculated drag on suspended tentacles of *Eupolyornia heterobranchia* increased with increasing velocity ( $F_{(1,76)} = 77.1$ ,  $P = 0.0001$ ,  $R^2 = 0.50$ ). Despite this relationship, linear regression analysis indicates that maximum tension (at the points of attachment) was independent of velocity (Fig. 3,  $F_{(1,76)} = 2.67$ ,  $P = 0.11$ ). Maximum tension in the tentacles was between  $0.34 \times 10^{-5}$  N and  $5.2 \times 10^{-5}$  N (mean =  $1.6 \times 10^{-5}$  N,  $n = 78$ ,  $\text{SE} = 0.10 \times 10^{-5}$  N). The results of linear regression analysis using data corrected for just  $C_{Dc}$  ( $F_{(1,76)} = 0.72$ ,  $P = 0.40$ ) as well as both  $C_{Dc}$  and  $d_c$  ( $F_{(1,76)} = 2.38$ ,  $P = 0.13$ ) are consistent with the results of linear regression analysis on the uncorrected data: maximum tension (at the points of attachment) remained independent of velocity.

Tension is a function not only of drag, but also of the ratio between the span and sag of the tentacle (Eqn 7). The independence of tension and velocity indicate that the ratio of span to sag ( $L/f$ ) should decrease as a function

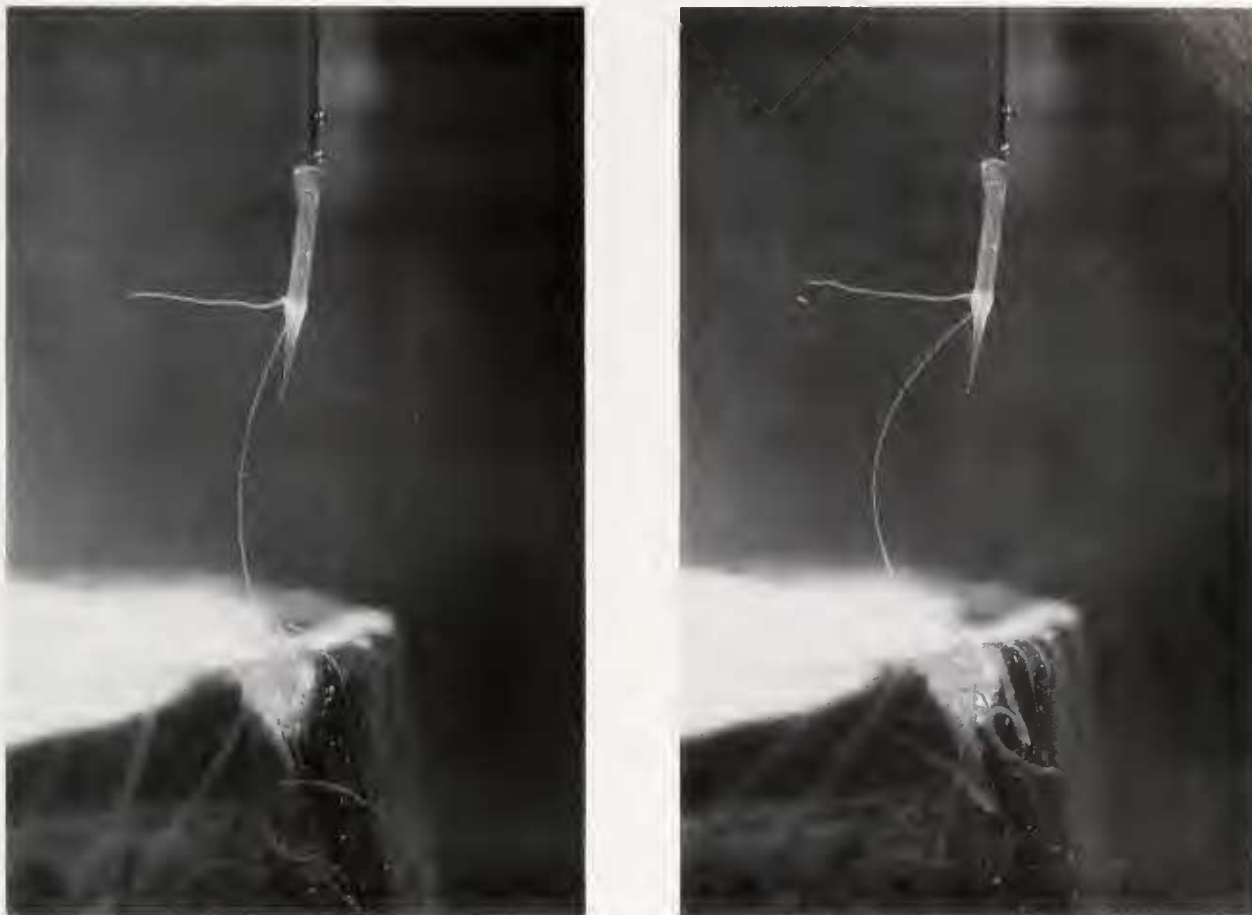
of increasing velocity. The relationship between velocity and ( $L/f$ ) is shown in Figure 4, where curve (a) on Figure 4 represents the linear regression of  $\ln(L/f)$  as a function of  $\ln(\text{velocity})$  plotted on linear axes. Linear regression analysis of  $\ln(L/f)$  with  $\ln(\text{velocity})$  demonstrates that ( $L/f$ ) decreased with increasing velocity ( $F_{(1,76)} = 90.1$ ,  $P = 0.0001$ ,  $R^2 = 0.54$ ).

This relationship could be created by some combination of increasing sag and decreasing span with increasing velocity. Although minimum span was set by the end of the probe, span deviated from this minimum as a terebellid behaviorally moved the point of attachment relative to the end of the probe. Accordingly, span varied between 13.3 and 47.2 mm (mean span = 29.4 mm,  $n = 78$ ,  $\text{SE} = 1.10$ ) and sag varied between 0.160 and 10.3 mm (mean sag = 3.32 mm,  $n = 78$ ,  $\text{SE} = 0.29$ ). Linear regression analysis on the  $\ln$ - $\ln$  relationship between variables reveals that while sag did increase significantly with velocity ( $F_{(1,76)} = 52.9$ ,  $P = 0.0001$ ,  $R^2 = 0.41$ ; for examples, see Fig. 5 and Fig. 6), span was independent of velocity ( $F_{(1,76)} = 1.18$ ,  $P = 0.28$ ).

Individual tentacles initially responded to increases in velocity by increasing sag over a number of seconds ( $<30$



**Figure 4.** The ratio of span-to-sag of suspended tentacles of *Eupolyornia heterobranchia* as a function of velocity ( $\text{m s}^{-1}$ ). Points indicate data. Line (a) indicates the regression from a  $\ln$ - $\ln$  plot of this data; linear regression analysis on  $\ln$ - $\ln$  transformed data indicates that span-to-sag decreased as a function of velocity. Line (b) indicates the theoretical relationship between ( $L/f$ ) and velocity when constant values of tension and span were used in Eqn 12 (means for the data set:  $1.57 \times 10^{-5}$  N and 0.0295 m, respectively).



**Figure 5.** Photograph of a tentacle of *Eupolyommia heterobranchia* suspended perpendicular to flow. The tip of the tentacle dangles in the direction of flow, which is from right to left. For scale, span of the tentacle in both photographs is 2.5 cm. The photograph on the left is taken just as the velocity in the flow tank is increased from 1.5 to 3 cm s<sup>-1</sup>. The photograph on the right is of the same tentacle taken several minutes after the increase in velocity. Tentacles respond to increasing velocity by increasing sag.

seconds;  $n = 13$  tentacles). After the initial increase in sag, relatively small increases and decreases in sag occurred while velocity remained constant (Fig. 6).

#### *Mechanical response of tentacles*

A typical force-extension curve for a tentacle of *E. heterobranchia* is shown in Figure 7 (obtained by tracing the result of one force-extension trial directly off the chart paper). A force of  $4.6 \times 10^{-4}$  N more than tripled the length of this tentacle ( $\lambda = 3.5$ ) before breakage. Tentacles broke at forces between  $0.68 \times 10^{-4}$  N and  $7.6 \times 10^{-4}$  N (mean =  $3.5 \times 10^{-4}$  N,  $n = 29$ , SE =  $3.1 \times 10^{-5}$  N). Tentacles broke at  $\lambda$ s ranging from 1.79 to 5.35 (mean = 3.34,  $n = 29$ , SE = 0.17).

The slope of this curve is a measure of the relative stiffness of the tentacle, or its resistance to being extended. The tentacles of *E. heterobranchia* are least stiff at low  $\lambda$ s, requiring relatively little force to extend (Fig. 7a); than at

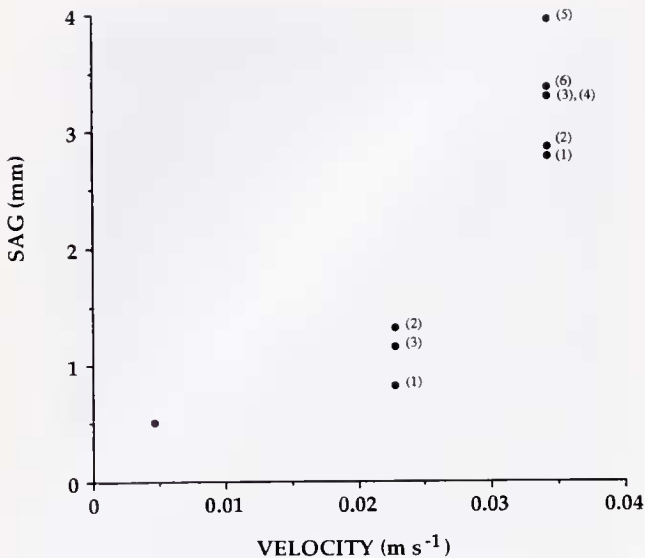
high  $\lambda$ 's (Fig. 7b). The transition in stiffness (*i.e.*, where the curve deviated from a line tangent to the lower portion of the curve; Fig. 7a) began at  $\lambda$ s in the range 1.66 to 2.48 (mean  $\lambda = 1.93$ ,  $n = 5$ , SE = 0.15) and at forces between  $0.18 \times 10^{-4}$  and  $0.64 \times 10^{-4}$  N (mean =  $0.36 \times 10^{-4}$  N,  $n = 5$ , SE =  $0.08 \times 10^{-4}$  N). Although these tentacles do exhibit strain rate dependent stiffness and stress-relaxation (*sensu* Vincent, 1990) at high  $\lambda$ s, these effects are not seen at low  $\lambda$ s (Johnson, unpubl. data).

The mean maximum tension in suspended tentacles was significantly less than the mean force at which stiffness increased (uncorrected data, ANOVA:  $F_{(1,82)} = 22.4$ ,  $P = 0.0001$ ).

#### **Discussion**

Tentacles of the terebellid polychaete *Eupolyommia heterobranchia* demonstrate a new mechanism of coping with flow forces. Sagging reduces flow-induced tension in ten-





**Figure 6.** Sag (mm) as a function of velocity ( $\text{m s}^{-1}$ ) for one tentacle of *Eupolyornia heterobranchia* that maintained a constant span (mean = 2.8 cm,  $n = 9$ ,  $\text{SE} = 1.15$ ) at  $0.005 \text{ m s}^{-1}$ ,  $0.023 \text{ m s}^{-1}$ , and  $0.034 \text{ m s}^{-1}$ . Small numbers indicate the order in which the tentacle was photographed at a specific velocity. Photographs were taken approximately 5 s apart. Tentacles respond to velocity by increasing sag over a number of seconds. Within a velocity sag may also decrease (e.g., 5  $\rightarrow$  6 at  $0.034 \text{ m s}^{-1}$ ) suggesting that muscles are actively involved in regulating sag in the tentacles.

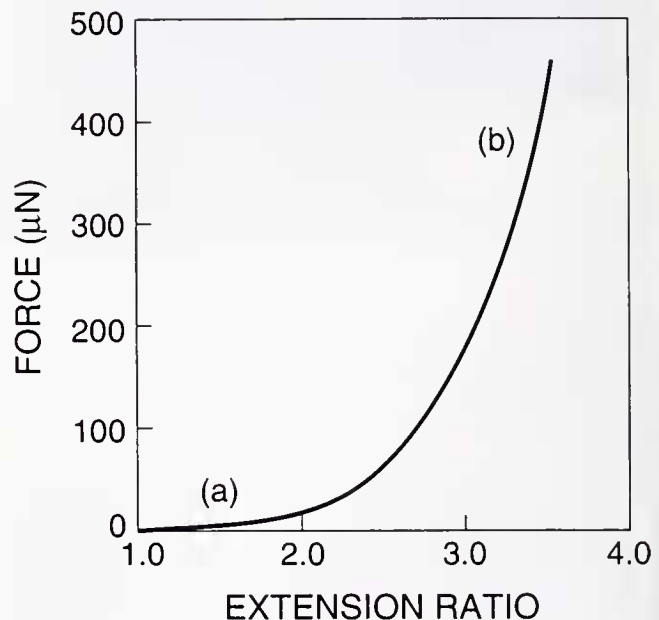
tacles; the largest contributor to this reduction in tension was achieved by closer alignment of force vectors that resist flow (parallel with the length of the tentacle) with force vectors imposed by flow (parallel with the direction of flow). This mechanism has the same ultimate effect as drag reduction by flexibility, streamlining, and reorientation: by modifying the effects of flow forces an organism can function in a wider range of flows (Wainwright and Dillon, 1969; Wainwright *et al.*, 1976; Koehl, 1977, 1984; Vogel, 1984; Denny *et al.*, 1985; Harvell and LaBarbera, 1985; Carrington, 1990). The discussion below analyzes the contribution of sagging and reorientation to tension experienced in the tentacles of *E. heterobranchia*.

The versatile, extensible, and flexible tentacles of terebellid polychaetes commonly occur adjacent to a substratum in low flow, mud, or sand flat environments (reviewed in Fauchald, 1977; Fauchald and Jumars, 1979). Such proximity to a substratum reduces the relative drag experienced for a given freestream flow because of the effect of the boundary layer (slower flows occur adjacent to the substratum). In contrast, the tentacles of the terebellid *E. heterobranchia*, extend not only over a substratum but also out into flow. Although extending tentacles into flow and over fronds of floating algae might increase access to potential food resources, this behavior also increases the exposure of tentacles to drag. Drag will have

conflicting mechanical consequences to tentacles, both positive, including facilitation of tentacle extension, as well as negative, including breakage or dislodgment.

Mechanical analysis, in which tentacles are modelled as the cables of suspension bridges (Eqn 7), reveals the behavioral and mechanical response of these tentacles to drag. For example, Eqn 7 shows that maximum tension in these tentacles (at the points of attachment) was a function not only of drag but also of the ratio between span and sag ( $L/f$ ). Maximum tension was statistically independent of drag, because increasing sag (shown by Figs. 5 and 6) decreased the ratio of span to sag and thus maintained a constant tension despite increasing velocity and, therefore, increasing drag.

Maximum tensions experienced by suspended tentacles were an order of magnitude less than the forces required to break the tentacles, indicating that suspended tentacles that sag are probably never in danger of being broken over the range of velocities at which they remained suspended. One can then ask: would tentacles in this orientation and in these flows break if they didn't sag? To examine this question, tension was calculated using Eqn (7) for tentacles of mean span, keeping ( $L/f$ ) constant over the range of velocities examined. Two extremes, the high-



**Figure 7.** Force ( $\mu\text{N}$ ) as a function of extension ratio ( $\lambda$ ) for a relaxed tentacle of *Eupolyornia heterobranchia*. The curve shown in this figure was obtained by tracing the result of one force-extension trial off the chart paper. The slope of this curve is a measure of the relative stiffness of the tentacle. (a) These tentacles are least stiff at the lowest strains, requiring relatively little force to extend; (b) tentacles are most stiff just prior to breakage. Comparison of this curve with tensions and  $\lambda$ s of sagging tentacles indicates that sagging involves active muscles and is not merely a consequence of the passive material properties of the tentacles.

est (150.75) and the lowest (4.54) obtained from this data set, were chosen for  $(L/f)$ . The curves (a) and (b), obtained from the highest and lowest  $L/f$  respectively, were superimposed on the experimental data (Fig. 3: the spans of the tentacles whose data points fall below line b were shorter than the mean tentacle span. Because span contributes not only to this ratio but also to drag, the consequent tension was lower than that obtained from the line calculated from mean span). It can be seen from these calculations that all values for tension obtained from the data are lower than they would be if the tentacles were allowed only a small sag (as in curve 3a). These low-sagging tentacles would be subjected to their mean breaking force of  $3.5 \times 10^{-4}$  N at  $0.053 \text{ m s}^{-1}$ , well below the highest velocity at which tentacles remained suspended perpendicular to flow ( $0.07 \text{ m s}^{-1}$ ). Thus, sagging allows tentacles to remain suspended without breakage at higher flows than would otherwise be possible.

Although sagging potentially avoids breakage, the force in suspended tentacles was an order of magnitude less than that which would break them, suggesting that some other explanation accounts for the particularly low level of tension in suspended tentacles. Perhaps the tentacles sagged passively until they reached an equilibrium between the force imposed on the tentacles and the force with which the material of the tentacles could resist further extension. This mechanism assumes that muscles played no active role in determining the extension of the tentacles. If the tentacles were sagging passively, then a given calculated tension should have produced an extension ratio similar to that produced by a given force for the relaxed tentacle in Figure 7. In fact, although calculated tensions for sagging tentacles were as high as  $5.2 \times 10^{-5}$  N, corresponding to  $\lambda \cong 2.5$  in Figure 7, the greatest  $\lambda$  for sagging tentacles was only  $\lambda = 1.12$ . Thus, tentacles extended too little to be sagging passively: active muscular control must have been involved in controlling sag in the tentacles. Further, suspended tentacles sometimes decreased their sag by as much as 15% when experiencing a constant flow (Fig. 6), also indicating that there is an active muscular contribution controlling sag.

Given that muscles actively control sag in the tentacles, could the observed mean maximum tension correspond to the peak isometric tension of the muscle? Although some invertebrate muscles are somewhat stronger, virtually all muscle exerts a maximum stress of  $0.5 \text{ MN m}^{-2}$  (Schmidt-Neilsen, 1983). One can estimate whether the stress in the tentacles exceeds the ability of muscles to hold tentacles in tension by dividing the mean maximum tension ( $1.6 \times 10^{-5}$  N) by an estimate of the cross-sectional area of the muscle in the tentacles ( $3.9 \times 10^{-8} \text{ m}^2$ ;  $n = 28$ ,  $SE = 0.9 \times 10^{-8} \text{ m}^2$ ; Johnson, 1992). The resulting estimate of stress in the muscles of suspended tentacles

( $4.1 \times 10^{-4} \text{ MN m}^{-2}$ ) is several orders of magnitude less than that which the muscles can maximally exert.

Thus, *E. heterobranchia* are modulating tension at such low levels in tentacles neither (1) to prevent breakage *per se*, nor (2) as a result of passive material properties of the tentacles, nor (3) because of the limits of peak isometric tension in their muscles. One question arises from these results: is there a functional significance to the level of tension actively maintained in suspended tentacles? The next obvious hypothesis is that *E. heterobranchia* maintain tension in their tentacles below the detachment strength of the mucus and cilia. This hypothesis remains to be tested.

#### *L/f as a function of velocity*

The shape of the relationship between  $(L/f)$  and velocity, described by the curve in Figure 4, suggests that relatively large changes in sag are required to modulate tension at low velocities; whereas relatively small changes in sag result in constant tension at higher velocities. What accounts for the shape of this relationship between  $(L/f)$  and velocity? To address this question, the theoretical relationship between  $(L/f)$  and velocity was determined using constant tension and span by rearranging Eqn (7) to solve for a theoretical  $(L/f)$  as indicated below:

$$\frac{L}{f} = \sqrt{64 \left( \frac{T}{D} \right)^2 - 16} \quad (12)$$

Mean values of tension and span (used in the calculation of  $D$ ) for the data set were used to determine these constants ( $1.57 \times 10^{-5}$  N and  $0.0295$  m, respectively). The result of this calculation is shown by curve (b) in Figure 4. Not surprisingly, comparison of curve (b) with curve (a) in Figure 4 illustrates the earlier statistical results: that these curves represent the sag that is necessary to mediate drag so that tension is modulated under conditions of constant span.

#### *Effects of tentacle orientation on drag*

The above theoretical calculations assumed a constant coefficient of drag and a constant diameter, independent of sag. The above results are thus independent of changes in  $C_D$  and  $d$  that will occur in a sagging tentacle. The following section examines the effects of changes in  $C_D$  and  $d$  to drag reduction (Fig. 3).

Drag on sagging tentacles should be lower than that of a non-sagging tentacle of equal span because tentacles thin as they sag and because portions of the tentacles are oriented at angles less than perpendicular to flow. To examine the potential contribution of sagging to drag reduction, tension was calculated, again using Eqn (7) and the highest and lowest  $L/f$ , but including  $C_{Dc}$  as the coefficient of drag and  $d_c$  as the diameter of these tentacles.



Calculations using the highest  $L/f$ ,  $C_{Dc}$  and  $d_c$  resulted in a line identical to (a); there was no significant drag reduction in a tentacle of such low sag. Calculations using the lowest  $L/f$  with either just  $C_{Dc}$  or both  $C_{Dc}$  and  $d_c$  resulted in curve (c). There are several points that are illustrated by these results: (1) sagging results in drag reduction, especially at high velocities and high sags, (2) drag reduction due to decrease in diameter with increasing sag is negligible, and (3) even at high sags, drag reduction by sag-related reduction in the coefficient of drag contributes much less to reduction of tension than structural alignment of force vectors, especially at low velocities.

An extreme case of orientation relative to flow occurs when tentacles are dangling (*i.e.*, the danglers shown in Fig. 2 and Fig. 5) and thus are oriented parallel to flow. Could a tentacle become long enough and flow fast enough that drag would be sufficient to extend, or even to break, tentacles dangling out into flow? Drag on tentacles oriented parallel to flow can be estimated as approximately half that of tentacles oriented perpendicular to flow (Vogel, 1981). Actual drag should be slightly higher than given by this estimate because tentacles are of finite length. For this reason, I call this estimate "theoretical minimum drag." Figure 8 shows the theoretical minimum drag as a function of velocity for danglers that are 1 cm, 10 cm, and 30 cm long (a reasonable range of lengths for the tentacles of *E. heterobranchia*). Danglers in the low-flow environment of an intertidal flat are never in danger of being broken by drag. When terebellids relax the longitudinal muscles in their tentacles, however, drag is sufficient to contribute to passive tentacle extension. For example, Figure 8 indicates that danglers that are 10 cm long in flow of  $0.10 \text{ m s}^{-1}$  (the lowest peak speed measured) experience forces ( $1.3 \times 10^{-5} \text{ N}$ ) that, while still within the low stiffness region of the force-extension curve, are sufficient to nearly double the length of the average relaxed tentacle (Fig. 7). This mechanism of passive tentacle extension is most effective for longer tentacles in faster flows.

#### Ecological consequences

Quite apart from the mechanical results of this study, the observation that *E. heterobranchia* individuals suspend their tentacles into flow suggests that they are using tentacles to supplement deposit feeding with the capture of suspended food particles. While I have not observed suspension feeding in *E. heterobranchia*, it seems unlikely that it would reject suspended food particles that intercept its suspended tentacles. Although most terebellids are entirely selective deposit feeders (Fauchald and Jumars, 1979), suspension feeding does contribute to the diet of the terebellid *Lanice conchilega* (Buhr, 1976; Buhr and Winter, 1977; Fauchald, 1977). Furthermore, other ter-

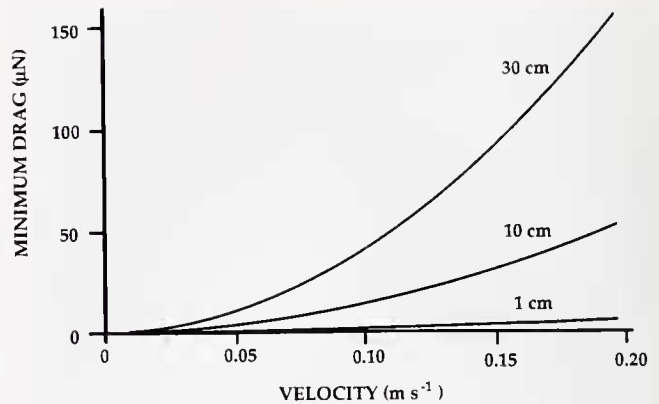


Figure 8. Theoretical minimum drag ( $\mu\text{N}$ ) as a function of velocity ( $\text{m s}^{-1}$ ) for 1 cm, 10 cm, and 30 cm long tentacles oriented parallel to flow (danglers). Maximum velocity of  $0.2 \text{ m s}^{-1}$  represents the maximum speed measured at False Bay (Pentcheff, unpub. data). Drag on danglers was always well below the maximum breaking force of tentacles ( $7.6 \times 10^{-4} \text{ N}$ ), but often within the range that would assist in passive extension of tentacles.

ebellids, such as *Loimia medusa* (Ellers, pers. comm.) also extend their tentacles into flow in a manner similar to that which I have described for *E. heterobranchia*.

Flow over the relatively protected area where *E. heterobranchia* is found, and particularly between the layers of *U. fenestrata*, will be slower than that measured by Pentcheff (see Materials and Methods). Furthermore, the angle of tentacles to flow will often be less than perpendicular. Thus, *E. heterobranchia* would be able to suspend tentacles into flow during most of the tidal cycle.

Sagging allows the tentacles to remain suspended in higher flows than would otherwise be possible, presumably increasing the amount of food these tentacles can gather. Feeding would be enhanced by the ability to sag not only because of increased access to suspended material but also because of increased access to food resources deposited upon the prodigious surface area of the stacked thalli of *U. fenestrata*. Thus, sagging increases the ecological range over which these terebellid polychaetes can function.

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### Literature Cited

- Abbott, I. H., and A. E. Von Duenhoff. 1959. *Theory of Wing Sections*. Dover Publications, Inc., New York. 693 pp.
- Buhr, K.-J. 1976. Suspension-feeding and assimilation efficiency in *Lanice conchilega* (Polychaeta). *Mar. Biol.* **38**: 373-383.
- Buhr, K.-J., and J. E. Winter. 1977. Distribution and maintenance of a *Lanice conchilega* association in the Weser Estuary (FRG), with special reference to the suspension-feeding behaviour of *Lanice conchilega*. *Biology of Benthic Organisms. 11th European Marine Biology Symposium*, Galway, Ireland 1976: 101-113.
- Carrington, E. 1990. Drag and dislodgment of an intertidal macroalga: consequences of morphological variation in *Mastocarpus papillatus* Kutzing. *J. Exp. Mar. Biol. Ecol.* **139**: 185-200.
- Denny, M. W., T. L. Daniel, and M. A. R. Koehl. 1985. Mechanical limits to size in wave-swept organisms. *Ecol. Monogr.* **55**: 69-102.
- Fauchald, K. 1977. *The Polychaete Worms. Definitions and Keys to the Orders, Families and Genera*. Natural History Museum of Los Angeles County, Los Angeles. 188 pp.
- Fauchald, K., and P. A. Jumars. 1979. The diet of worms: a study of polychaete feeding guilds. *Oceanogr. Mar. Biol. Ann. Rev.* **17**: 193-284.
- Harvell, C. D., and M. LaBarbera. 1985. Flexibility: a mechanism for control of local velocities in hydroid colonies. *Biol. Bull.* **168**: 312-320.
- Hoerner, S. F. 1965. *Fluid-Dynamic Drag*. Hoerner Fluid Dynamics, Bricktown, NJ.
- Johnson, A. S. 1992. Morphology, mechanics and behavior in feeding with stretchy worm tentacles. *Am. Zool.* **32**: 116A.
- Koehl, M. A. R. 1977. Effects of sea anemones on the flow forces they encounter. *J. Exp. Biol.* **69**: 87-105.
- Koehl, M. A. R. 1984. How do benthic organisms withstand moving water? *Am. Zool.* **24**: 57-70.
- Price, L. H., and J. Hylleberg. 1982. Algal-faunal interactions in a mat of *Ulva fenestrata* in False Bay, Washington. *Ophelia* **21**: 75-88.
- Schmidt-Neilsen, K. 1983. *Animal Physiology: Adaptation and Environment* (3rd ed.). Cambridge University Press, Cambridge. 619 pp.
- Steinman, D. B. 1942. Suspension bridges. Pp. 289-358 in *Movable and Long-span Steel Bridges*, G. A. Hool and W. S. Kinne, eds. McGraw-Hill, New York.
- Vincent, J. 1990. *Structural Biomaterials*. Princeton University Press, Princeton, NJ. 244 pp.
- Vogel, S. 1981. *Life in Moving Fluids*. Willard Grant Press, Boston, MA. 352 pp.
- Vogel, S. 1984. Drag and flexibility in sessile organisms. *Am. Zool.* **24**: 37-44.
- Vogel, S., and M. LaBarbera. 1978. Simple flow tanks for research and teaching. *BioScience* **28**: 638-643.
- Wainwright, S. A., W. D. Biggs, J. D. Currey, and J. W. Gosline. 1976. *Mechanical Design in Organisms*. Princeton University Press, Princeton. 423 pp.
- Wainwright, S. A., and J. R. Dillon. 1969. On the orientation of sea fans. *Biol. Bull.* **136**: 130-139.